



Do arctic and red foxes compete for food?

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Abstract

Overlap and differences in food habits between arctic and red foxes, *Alopex lagopus* and *Vulpes vulpes*, were studied by collecting scats (faeces) at dens above the tree line (alpine region) in northern Norway. Factors other than fox species included den, region, year, height above the sea level, height above the tree line, distance to the tree line, and reproductive status. A total of 5314 scats was analysed, giving $n = 34$ and $n = 33$ “den-years” for arctic and red foxes, respectively. Lemming, voles, reindeer, and birds, were major prey of both fox species, and insects were frequent in red fox scats. Small mammals contributed 78% in both arctic and red foxes diet. Arctic foxes consumed more lemmings than red foxes, while red foxes consumed more voles, birds, and insects. Despite such differences, overlap in food habits between the two fox species was high, and consequently, competition for food is likely. Some of the differences may have been caused by environmental rather than intrinsic factors, as red foxes on average occupied dens at lower altitudes than arctic foxes. A high degree of variation was found within fox species, as well as within and between dens, years, and regions. Fox species was most important for the percentage of prey, year and region had smaller effects. The percentage of prey was correlated with height above sea level and height above the tree line as expected, except between the latter and lemming. Competition for food could be one important factor explaining the apparent exclusion of the threatened arctic fox from the home range of the abundant red fox.

Key words: *Alopex lagopus*, *Vulpes vulpes*, diet comparison, Norway

Introduction

Competition between related mammalian carnivores appears to be common, with the larger species generally superior to the smaller (e.g., LAMPRECHT 1978; SCHMIDT 1986; THEBERGE and WEDELES 1989; JOHNSON and FRANKLIN 1994; CAVALLINI and NEL 1995; PALOMARES and CARO 1999). The larger predator may affect the distribution, habitat use, feeding habits, group size, or activity patterns of the smaller predator. Only rarely may two similar-sized predators with similar diet coexist, as, e.g., the badger *Meles meles* and the red fox *Vulpes vulpes* (CIAMPALINI and LOVARI 1985; FEDRIANI et al. 1999), and perhaps also the red fox and the grey fox *Urocyon cinereoargenteus* (HOCKMAN and CHAPMAN 1983). Direct evidence of competition is difficult to prove without doubt. One set of conditions for ungulates may be that habitat and food overlap exist, and that the shared dietary resources are limited (PUTMAN 1996). This is more difficult for territorial carnivores where interspecific exclusion also takes place, because often only the result of the process of exclusion can be studied and not the process in itself.

The arctic fox *Alopex lagopus* in Fennoscandia (Norway, Sweden, and Finland) is very rare and threatened by extinction, whereas the red fox thrives throughout the re-

gion. Numerous discussions have pointed to the red fox as a competitor or even predator of the arctic fox (sensu HERSTEINSSON et al. 1989), but the relationship between the two species in the region is still largely unknown. Arctic foxes are restricted to alpine environments, and although a few are still found in most regions, breeding is very rare. Competition for food by the two fox species has been indicated, but lack of data has precluded reliable conclusions (sensu FRAFIJORD 1995). Arctic foxes feed largely on lemmings (reviewed by FRAFIJORD 1995; compare TANNERFELDT and ANGERBJÖRN 1998; ANGERBJÖRN et al. 1999; ELMHAGEN et al. 2000), but spatial and seasonal diet may vary greatly (e.g., FAY and STEPHENSON 1989; FRAFIJORD 1993; ANGERBJÖRN et al. 1994; BANTLE and ALISAUSKAS 1998; STRAND et al. 1998 a). The red fox lives in a diversity of habitats and its diet varies tremendously, but small mammals tend to be important (e.g., LUND 1962; HEWSON and KOLB 1975; JENSEN and SEQUEIRA 1978; CALISTI et al. 1990; CAVALLINI and LOVARI 1991).

The aim of this study is to investigate the food habits of sympatric arctic and red foxes in the alpine region of northern Norway. The main objective is to examine the degree of difference and overlap in the diet of the two fox species.

Material and methods

During the years 1994–1998 arctic fox dens throughout northern Norway were visited for examination and documentation (north of 65°N), and for recording the presence or absence of arctic foxes and arctic fox litters. Presence of red foxes at arctic fox dens was also recorded, as well as all red fox dens found at or above the tree line. I collected fox scats at dens whenever possible, and some samples were also collected by local wardens (Statskog–Fjelltjenesten). The scats were stored in a freezer and dried at 80–100°C for several hours until completely dry. Each scat was broken up by hand and its content identified according to FRAFIJORD (1995). The identification was mainly based on hairs and feathers, with only marginal, additional help from teeth and bones. Hairs from scats were compared under the microscope with hairs from a reference collection made previously. Small mammals (lemmings and voles) were identified on the coloration of the hairs. Focus was placed on the four major prey groups earlier identified as the most important to arctic and red foxes: lemmings, voles, reindeer *Rangifer tarandus* (from carcasses, some hair fragments are almost always ingested), and birds. Although other prey was also identified whenever possible, the scat content was not searched as thoroughly as previously (FRAFIJORD 1995) for minor prey items, and a smaller number of samples was studied under the microscope. Consequently, rare or minor prey are likely underestimated slightly in this study (sensu REYNOLDS and AEBISCHER 1991; CAVALLINI and VOLPI 1995). Single fox hairs were ignored, as well as plant material other than berries. No attempts were made to identify shrew (Soricidae) hairs, and only a single shrew mandible was found. No distinction was made between *Mustela erminea* and *M. nivalis*, both are included under the heading *Mustela e/n* (only *M. erminea* were found dead at dens). The mink *M. vison* and hare *Lepus timidus* are also potential prey. Possible voles include *Microtus agrestis*, *M. oeconomus*, *Clethrionomys rufocanus*, *C. rutilus*, and *C. glareolus*. *M. oeconomus* and *C. rutilus* have not been recorded from the south region, the only region where *C. glareolus* has been recorded. A category of “unidentified mammals” is not included in any statistical analysis.

Although the major aim of this study was to compare the food habits of red and arctic foxes, several other factors are included: litter of pups vs. no litter, year of collection, region, meter above sea level, meter above the tree line (nearest forest), and shortest distance to the nearest forest. The three latter factors were taken from topographical maps (1:50 000). Northern Norway was divided into four regions (Fig. 1): south (most of Nordland county), central (northern part of Nordland and a large part of Troms county), north (northern part of Troms and western part of Finnmark county) and northeast (eastern part of Finnmark). Year of collection was only used to give an indication of yearly differences, because in many cases the exact year of deposition of the scats was not known (older scats could perhaps be 1–3 years old). Evidence of reproduction was found either by observing pups or by tracks and signs at the den. Species inhabiting the den was recorded by observations or by signs on the den (notably the size of the entrances used). Two arctic fox dens were excluded from all analysis because the inhabiting species was uncertain.

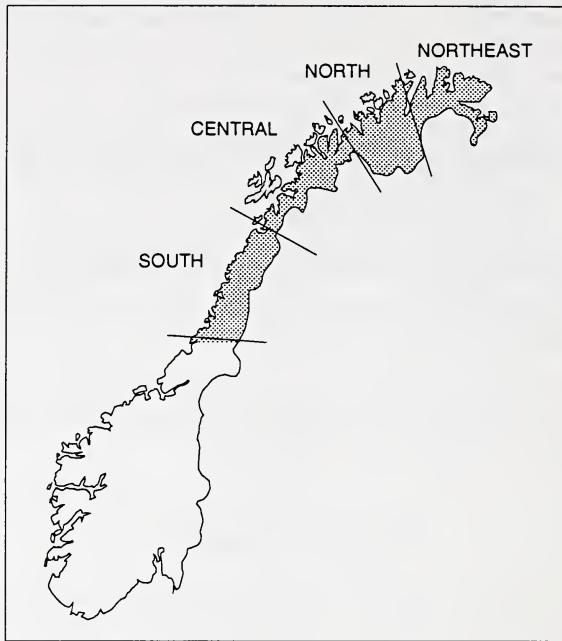


Fig. 1. Map of Norway, showing northern Norway (hatched) with the four regions indicated. Note that the arctic fox distribution range is smaller than the hatched area.

A minimum sample size of 30 scats was attempted, but two cases of smaller samples were included (27 and 28 scats, for the red fox). Smaller samples were lumped by species and region and included in some analyses if the number then exceeded 30 scats. Repeated sampling from the same den during several years was included in the analysis as different den-years. This concerned mostly six arctic fox dens, which were also treated separately. This gave a maximum number of samples (den-years) of 34 for arctic foxes and 33 for red foxes, with average sample sizes (\pm SD) of 82.5 ± 60.2 and 76.0 ± 43.1 scats, respectively. The total number of scats analysed was 2805 and 2509 for arctic and red foxes, respectively. Differences in food habits were tested by the Mann-Whitney U/Wilcoxon rank sum test (z-score) and Kruskal-Wallis H test (χ^2). Univariate ANOVA was used to indicate the relative importance of several factors (F), and Pearson's correlation coefficient (r) was used to study the relationship between prey types and several factors. Only frequency of occurrence is used. The percent of occurrence of every prey identified is given, but included in subsequent analysis are only prey with a frequency of occurrence in at least one fox species of more than 2%, and in most cases 5%. The latter includes only the four major prey items, with the addition of insects. Two indices were calculated to illustrate the magnitude of overlap and difference: percentage overlap (PO = Schoener overlap index; KREBS 1989, p. 381), and difference ($D = \sum |px_i - py_i|$, $i = 1 \dots 5$, px_i = percent of prey i in fox species x , py_i = percent of prey i in species y). In both, only the five most frequent prey were included. PO ranges from 0–100% overlap, D increases with increasing difference in food habits.

Results

Lemming, voles, reindeer, and birds were the major food of both arctic and red foxes, comprising 96 and 92% of the total (100%), respectively. Significant differences in food habits between arctic and red foxes were found for lemming, voles, birds, insects, and berries (Tab. 1), but not for reindeer, bird eggs or hare ($D = 93.0\%$, $PO = 61.8\%$). Arctic foxes consumed nearly twice as many lemmings as red foxes, and only about a fourth the

amount of voles. Thus, arctic foxes consumed many more lemmings than voles, while red foxes consumed about equal amounts of lemmings and voles (Tab. 1). Combining lemming and voles, the amounts of small mammals eaten were identical in arctic and red foxes, 78.0 and 78.2%, respectively. Red foxes consumed more birds, insects, and berries than arctic foxes, and appeared to have a more varied diet. Surprisingly, the amount of reindeer eaten was not significantly different despite the fact that the difference between the means was nearly 10%. Large standard deviations of the averages for the five major prey (Tab. 1) indicates large variation among dens within both arctic and red foxes. This was supported by the great range in the percentages for these prey items (Tab. 2). Maximum percentage of lemmings consumed by red foxes was more than 90%, and maximum percentage of voles consumed by arctic foxes was more than 50%. The maximum percentage of birds consumed was equal for arctic and red foxes (Tab. 2).

The number of samples varied greatly among regions and years, and several analyses were performed to outline the importance of the various factors. In one analysis, the samples were not divided by species, but by den, i. e., arctic ($n = 51$) or red fox ($n = 16$) dens (many red foxes inhabited arctic fox dens). The differences in the amount of prey eaten were much smaller compared to the results in table 1, with $D = 55.5\%$ and $PO = 79.3\%$. Significant differences were still found for lemmings ($z = 2.22$, $p = 0.03$), voles ($z = 2.46$, $p = 0.01$) and birds ($z = 2.89$, $p = 0.004$).

In north Norway, the tree line grows progressively higher from north to south, from sea level in the subarctic northeastern corner to ca. 750 m in the far south. The correlation coefficients were higher for meter a. s. l. than for meter above tree line in all but one

Table 1. Frequency of occurrence (%) of prey in scats from arctic and red foxes, and test between the two fox species. (Unident. m. = unidentified mammals).

	Arctic fox		Red fox		z	p
	Mean	SD	Mean	SD		
Lemming	66.1	21.5	37.5	23.2	4.35	0.000
Voles	11.9	10.3	40.8	27.0	4.97	0.000
Reindeer	28.8	23.9	19.5	18.4	1.64	0.10
Birds	10.0	14.9	31.6	17.8	5.19	0.000
Insects	1.0	2.1	5.5	8.3	3.92	0.000
Bird eggs	1.2	2.7	0.9	1.7	0.39	0.70
Hare	1.9	3.3	1.1	1.7	0.71	0.48
<i>Mustela e/n</i>	0.4	1.2	0.5	1.5	–	
Mink	0.0	0.0	0.3	1.6	–	
Fox	0.3	1.1	0.6	1.3	–	
Shrew	0.0	0.0	0.04	0.2	–	
Berries	0.03	0.2	1.3	2.8	2.82	0.005
Unident. m.	0.0	0.0	0.3	1.3	–	

Table 2. Minimum and maximum percentages of the five major prey for arctic and red foxes.

	Arctic fox		Red fox	
	Min.	Max.	Min.	Max.
Lemming	12.0	94.9	0.9	90.8
Voles	1.5	54.5	3.3	91.8
Reindeer	1.4	88.0	0.0	68.1
Birds	0.0	73.7	2.6	73.4
Insects	0.0	10.1	0.0	43.7

prey (Tab. 3), and lemming was not significantly correlated with meter above tree line. Voles, birds, and insects were negatively correlated with these two factors. The percentages of prey consumed were not correlated with distance to the tree line for any prey (Tab. 3). The majority of the insects found in scats was dung beetles *Aphodius* sp. (Scarabaeidae), but a few other species were also recorded. No correlation between the percentages of insects and reindeer (i. e. carrion) was found ($r = -0.12$, $p > 0.05$, $n = 67$).

When separating arctic and red foxes in the same analysis, only four significant relationships were found. For arctic foxes ($n = 31$), insect prey was related to m a.s.l. ($r = -0.38$, $p = 0.03$), whereas reindeer ($r = 0.47$, $p = 0.008$) and birds ($r = -0.42$, $p = 0.02$) were related to m a.t.l. For red foxes, lemming was related to m a.s.l. ($r = 0.38$, $p = 0.04$, $n = 29$).

In some cases arctic foxes were known to breed or it could be concluded that a litter was born recently. No significant difference was found in the percentages of the five major prey items from arctic fox dens with ($n = 10$) and without ($n = 24$) recent litters ($p > 0.05$), $D = 20.9\%$, $PO = 91.1\%$. In the red fox ($n = 22$ dens with litters and $n = 11$ dens without litters), significantly more scats at dens with pups contained insects (7.1 ± 9.6 vs. 2.3 ± 3.0 . $z = 2.01$, $p < 0.048$). The difference was nearly significant for reindeer ($z = 1.87$, $p = 0.06$), and not significant for lemming, voles, and birds ($D = 32.4\%$, $PO = 89.9\%$). Large standard deviations of the percentages indicate great variation among dens.

The red fox used old arctic fox dens, but also made its own den. Arctic fox dens ($n = 48$) were situated higher up in the mountains than red fox dens ($n = 12$, lack of accurate position of some dens reduced the sample size) (m a.s.l.: $z = 2.93$, $p = 0.003$; m a.t.l.: $z = 2.88$, $p = 0.004$) but not more distant to treeline (D t.l.: $z = 1.12$, $p = 0.3$). A similar result was found when considering the fox species that inhabited the den (Tab. 4). Arctic foxes lived much higher in the mountains than most red foxes, which is likely to influence prey availability and consumption. One test of the significance of altitude was to compare food of red foxes in arctic ($n = 16$) and red fox ($n = 17$) dens, but no significant difference was found ($p > 0.05$ for all five major prey; $D = 19.2$, $PO = 94.1\%$). The actual figures were opposite to what could be expected, with less lemmings and more voles and birds in red fox scats from arctic fox dens.

Table 3. Correlations between percentages of the five major prey and meter a.s.l. (m a.s.l.), meter above the tree line (m a.t.l.), and distance to the tree line (D t.l.). Arctic and red foxes combined ($n = 59-60$). ** $p < 0.01$, * $p < 0.05$.

	m a. s. l.	m a. t. l.	D t. l.
Lemming	0.42**	0.08	0.17
Voles	-0.56**	-0.34**	-0.14
Reindeer	0.26*	0.42**	-0.03
Birds	-0.51**	-0.39**	0.02
Insects	-0.46**	-0.31*	-0.17

Table 4. Meter above sea level (m a.s.l.), meter above tree line (m a.t.l.), and distance to tree line (D t.l., km) for dens inhabited by arctic ($n = 31$) and red foxes ($n = 29$) and subject to scat collection.

	Arctic fox		Red fox		z	p
	Mean	SD	Mean	SD		
m a. s. l.	859.7	189.9	557.8	194.9	5.26	0.000
m a. t. l.	241.0	117.5	104.1	84.3	4.05	0.000
D t. l.	8.0	4.0	6.8	4.1	1.35	0.18

Table 5. Numbers of samples (den-years) collected by year and region in arctic and red foxes.

Year	Arctic fox	Red fox
1994	7	7
1995	9	2
1996	4	1
1997	1	8
1998	10	11
Region		
South	20	4
Central	9	9
North	3	16
Northeast	2	4

Table 6. Univariate analysis of the significance of the various factors for the percentages of lemming, voles, reindeer and birds in fox scats.

	Lemming		Voles		Reindeer		Birds	
	F	p	F	p	F	p	F	p
Year	1.70	0.2	13.67	0.001	12.41	0.001	4.01	0.05
Region	0.51	0.5	0.90	0.4	7.70	0.008	0.00	1.0
m a. s. l.	1.39	0.2	4.20	0.05	1.86	0.2	0.12	0.7
m a. t. l.	9.07	0.004	3.33	0.07	1.67	0.2	0.03	0.9
D t. l.	7.46	0.009	2.30	0.1	4.02	0.05	0.15	0.7
Species	11.22	0.002	11.92	0.001	1.25	0.3	9.80	0.003

The samples were skewed among regions and somewhat among years (Tab. 5), and further analyses of these factors were difficult. This was also complicated by the fact that the scats could not always be identified to the correct year of deposition. Instead of analysing these factors separately, all factors were included in a tentative analysis to give an idea of the relative importance of the various factors for the percentage of prey in scats. The significance of the factors varied for the four major prey items (Tab. 6). Fox species was important for lemming, voles, and birds, but not for reindeer. Year was important for voles and reindeer, and region only for reindeer. M a. s. l. was least important. M a. t. l. and D t. l. were significant for lemming (Tab. 6). Thus, fox species and year were the most important of the factors tested.

For a better understanding of the effects of year and den, six arctic fox dens inhabited by arctic foxes with repeated sampling over several years ($n = 15$ den-years) were analysed separately. The percentage of lemming ($\chi^2 = 10.20$, $p = 0.04$, d. f. = 4) varied significantly across years, but not voles, reindeer or birds ($p > 0.05$). No significant variation across the six dens was found. Relatively high variances indicated large variation both within dens and years. As example, for a single den, minimum and maximum percentages of lemming were 12.0 and 77.5 (variance = 1189.8). For the single most extreme year, minimum and maximum lemming were 12.0 and 71.3%, respectively (variance = 544.1).

Discussion

Although significant differences in food habits were found, arctic and red foxes had a high overlap and are likely to compete for the same food. Arctic foxes relied heavily on

lemmings and reindeer carcasses, while red foxes consumed about equal amounts of lemmings, voles and birds, but less reindeer. Do the red fox have a broader niche and is the arctic fox more a specialist hunter? A large variation in food habits was found within the two fox species, both within and between dens, years, and regions. This variation is, of course, mostly related to the lemming and vole cycles (*sensu* ELMHAGEN *et al.* 2000). During this study period, no great lemming or vole years were experienced in the mountain region, but one year in the central region and two years in the south region had smaller maxima.

The proportions of lemming, voles, reindeer, and birds in the fox diet were related to the height above sea level or above the tree line, consistent with what could be expected, except that lemming was not related to the height above the tree line. Red foxes were on average found in lower areas than arctic foxes. Furthermore, the samples were collected over a large area (north Norway) and over several years, and were not evenly distributed among years and regions. The numbers of voles and birds are supposed to decrease with altitude, much more than the numbers of lemming and reindeer. Consequently, a large portion of the difference in food habits between arctic and red foxes was probably related more to external (environmental) than internal factors. Thus, one may conclude that arctic and red foxes have a high degree of overlap in food habits and will compete for food. Arctic foxes appear to rely more heavily on lemmings than red foxes at similar altitude, and are perhaps a little less opportunistic than red foxes.

Fox species affected the percentages of prey consumed most, and year of collection, region, height above sea level or tree line, and distance to the tree line less. Height above the sea level was thought to be poorly related to the proportion of the different foods consumed in north Norway. Height above the tree line varies less with latitude and should be better related to food habits. But the correlations between the percentages of prey and height above sea level were better than with height above tree line. This result is surprising and difficult to explain. It may have resulted inadvertently from the geographically skewed collection of scats, most arctic fox litters and scats were found in the south, while most red fox litters and scats were found in the north.

In southern Norway (FRAFJORD 1995), both arctic and red foxes had consumed almost exclusively (min. 95%) small mammals (lemming and voles), and in another study 85% (STRAND *et al.* 1998a), compared to 78% in this study. Reindeer were notably a larger part of the diet in northern Norway. Some of the samples from north Norway probably included scats from the winter season, when foxes may eat more reindeer carrion. A high mortality among the domestic reindeer in some regions and some years, may have supplied the foxes with additional food than normally available. (Most slaughter offal is today transported away from the mountains to permanent deposits.) This may also have resulted in the birth of some arctic fox litters in years of low numbers of small mammals. A sample of 98 arctic fox winter scats collected at three neighbouring dens in the central region in April 1998, gave frequencies of occurrence of 80.6% lemming, 15.3% voles, 9.2% reindeer, and 10.2% birds. This does not support the hypothesis of a larger proportion of reindeer in the winter diet, but this proportion is likely to vary greatly according to availability (compare STRAND *et al.* 1998a). In the northeastern region in 1999, 58 red fox scats were collected close to cliffs where sea birds nested (not at dens). These foxes consumed almost exclusively birds, *i.e.*, comparable to arctic foxes in Svalbard (FRAFJORD 1993): 94.8% birds, 1.7% lemmings, 5.2% voles, and 3.4% reindeer. Obviously, when such opportunistic predators are concerned, large numbers of samples from different regions and years are needed to give a complete picture of their diet.

In this study, I attempted to collect and analyse relatively large samples for each den, and to have a comparatively large number of dens for both fox species (*sensu* REYNOLDS and AEBISCHER 1991), but the sample size was still not sufficient for detailed regional and yearly analysis. Although there are inherent difficulties with the accuracy of scat analysis

(CAVALLINI and VOLPI 1995), these should not affect the comparisons made in this study since all analyses were made in the same manner. However, the method used may possibly underestimate the proportion of voles compared to lemming, and more so at higher percentages of lemmings. The majority of insects found in scats was dung beetles. Some of the beetles may not have been eaten by foxes, and it could be speculated that the larvae had metamorphosed inside the scat (some beetles were indeed undamaged). Other explanations could be that the fox had accidentally (by eating dung) ingested or deliberately eaten the beetles. In one case, a number of dung beetles were found in the few remains of a small fox pup, which indicates that these beetles may also be scavengers. The only berry that is found to any great amount in these alpine regions is *Empetrum hermaphroditum*, its low nutritional value may explain the low frequency of berries in scats. Faeces containing a large number of fox hairs indicate cannibalism.

Despite significant differences in the proportions of the major food items in the diet of red and arctic foxes, the large diet overlap makes competition very likely although it is not strictly a proof (sensu PUTMAN 1996). Although the ranges of the two fox species overlap, this does not necessarily mean that competition is direct. An indirect competition where red foxes exclude arctic foxes from the more productive habitats (which are limited in the alpine region) is more likely (sensu SMITS et al. 1989; HERSTEINSSON and MACDONALD 1992; STRAND et al. 1998 b). Such an exclusion, or interspecific territorialism, may consequently also work in years (or seasons, habitats) when the dietary resources are not limiting. The red fox may consider an arctic fox as just another, but smaller and inferior, red fox. Competition for food may be the single most important factor involved in the red fox's exclusion of the arctic fox, which may, eventually, lead to the extinction of the arctic fox in Fennoscandia.

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Zusammenfassung

Konkurrieren Polarfüchse und Rotfuchs um Nahrung?

Überlappung und Unterschiede in der Zusammensetzung der Nahrung zwischen Polar- und Rotfuchs, *Alopex lagopus* und *Vulpes vulpes* wurden über Kotanalysen von Bauen oberhalb der Baumgrenze in Nord-Norwegen untersucht. Außer den Fuchsspecies wurden zusätzlich die Faktoren Bau, Region, Jahr, Höhe über Meeresspiegel, Höhe oberhalb der Baumgrenze, Entfernung zur Baumgrenze und Reproduktionsstatus analysiert. Insgesamt standen 5314 Kotproben zur Verfügung in n = 34 und n = 33 „Bau-Jahren“ für Polar- bzw. Rotfuchs. Lemminge, Wühlmäuse, Rentiere und Vögel waren Hauptbeute von beiden Fuchsarten, und Insekten waren in Rotfuchskot häufig. Kleinsäuger machten 78% der Nahrung bei beiden Arten aus. Polarfüchse erbeuteten mehr Lemminge als die Rotfüchse, während Rotfüchse mehr Wühlmäuse, Vögel und Insekten verzehrten. Trotz dieser Unterschiede war die Überlappung im Nahrungsspektrum beider Arten groß, und Nahrungskonkurrenz ist wahrscheinlich. Einige der Unterschiede könnten eher durch Umweltbesonderheiten bedingt sein, da Rotfüchse durchschnittlich Baue in geringeren Höhenlagen bewohnten als Polarfüchse. Ein hoher Variationsgrad ergab sich innerhalb der Fuchsarten aber auch innerhalb und zwischen Bauen, Jahren, und Regionen. Die Besonderheiten der Fuchsart war jedoch hauptsächlich bedeutend für die prozentuale Nahrungs-

zusammensetzung, Jahr und Region hatten geringeren Effekt. Die prozentuale Nahrungszusammensetzung war wie erwartet mit der Höhe über dem Meeresspiegel und der Höhe über der Baumgrenze korreliert, ausgenommen zwischen letzterem und Lemmings. Nahrungskonkurrenz könnte daher ein wichtiger Faktor zur Erklärung der anscheinenden Verdrängung des Polarfuchses aus dem Wohngebiet des überzähligen Rotfuchses sein.

References

- ANGERBJÖRN, A.; HERSTEINSSON, P.; LIDÉN, K.; NELSON, E. (1994): Dietary variation in arctic foxes (*Alopex lagopus*) – an analysis of stable carbon isotopes. *Oecologia* **99**, 226–232.
- ANGERBJÖRN, A.; TANNERFELDT, M.; ERLINGE, S. (1999): Predator-prey relationships: arctic foxes and lemmings. *J. Anim. Ecol.* **38**, 34–39.
- BANTLE, J. L.; ALISAUSKAS, R. T. (1998): Spatial and temporal patterns in arctic fox diet at a large goose colony. *Arctic* **51**, 231–236.
- CALISTI, M.; CIAMPALINI, B.; LOVARI, S.; LUCHERINI, M. (1990): Food habits and trophic niche variation of the red fox *Vulpes vulpes* (L., 1758) in a Mediterranean coastal area. *Rev. Ecol. (Terre Vie)* **45**, 309–320.
- CAVALLINI, P.; LOVARI, S. (1991): Environmental factors influencing the use of habitat in the red fox, *Vulpes vulpes*. *J. Zool. (London)* **223**, 323–339.
- CAVALLINI, P.; NEL, J. A. J. (1995): Comparative behaviour and ecology of two sympatric mongoose species (*Cynictis penicillata* and *Galerella pulverulenta*). *S. Afr. Tydskr. Dierk.* **30**, 46–49.
- CAVALLINI, P.; VOLPI, T. (1995): Biases in the analysis of the diet of the red fox *Vulpes vulpes*. *Wildl. Biol.* **1**, 243–248.
- CIAMPALINI, B.; LOVARI, S. (1985): Food habits and trophic niche overlap of the badger (*Meles meles* L.) and the red fox (*Vulpes vulpes* L.) in a Mediterranean coastal area. *Z. Säugetierkunde* **50**, 226–234.
- ELMHAGEN, B.; TANNERFELDT, M.; VERUCCI, P.; ANGERBJÖRN, A. (2000): The arctic fox (*Alopex lagopus*): an opportunistic specialist. *J. Zool. (London)* **250**, (in press).
- FAY, F. H.; STEPHENSON, R. O. (1989): Annual, seasonal, and habitat-related variation in feeding habits of the arctic fox (*Alopex lagopus*) on St. Lawrence Island, Bering Sea. *Can. J. Zool.* **67**, 1986–1994.
- FEDRIANI, J. M.; PALOMARES, F.; DELIBES, M. (1999): Niche relations among three sympatric Mediterranean carnivores. *Oecologia* **121**, 138–148.
- FRAJFJORD, K. (1993): Food habits of arctic foxes (*Alopex lagopus*) on the western coast of Svalbard. *Arctic* **46**, 49–54.
- FRAJFJORD, K. (1995): Summer food habits of arctic foxes in the alpine region of southern Scandinavia, with a note on sympatric red foxes. *Ann. Zool. Fennici* **32**, 111–116.
- HERSTEINSSON, P.; MACDONALD, D. W. (1992): Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64**, 505–515.
- HERSTEINSSON, P.; ANGERBJÖRN, A.; FRAJFJORD, K.; KAIKUSALO, A. (1989): The arctic fox in Fennoscandia and Iceland: Management problems. *Biol. Conserv.* **49**, 67–81.
- HEWSON, R.; KOLB, H. H. (1975): The food of foxes (*Vulpes vulpes*) in Scottish forests. *J. Zool. (London)* **176**, 287–292.
- HOCKMAN, J. G.; CHAPMAN, J. A. (1983): Comparative feeding habits of red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) in Maryland. *Am. Midl. Nat.* **110**, 276–285.
- JENSEN, B.; SEQUEIRA, D. M. (1978): The diet of the red fox (*Vulpes vulpes* L.) in Denmark. *Dan. Rev. Game Biol.* **10**, 1–16.
- JOHNSON, W. E.; FRANKLIN, W. L. (1994): Spatial resource partitioning by sympatric grey fox (*Dusicyon griseus*) and culpeo fox (*Dusicyon culpaes*) in southern Chile. *Can. J. Zool.* **72**, 1788–1793.
- KREBS, C. J. (1989): *Ecological methodology*. New York: Harper Collins Publishers.
- LAMPRECHT, J. (1978): The relationship between food competition and foraging group size in some larger Carnivores. *Z. Tierpsychol.* **46**, 337–343.
- LUND, HJ. M.-K. (1962): The red fox in Norway. II. The feeding habits of the red fox in Norway. *Medd. Statens Viltund.*, 2. Serie, **12**, 1–79.
- PALOMARES, F.; CARO, T. M. (1999): Interspecific killing among mammalian carnivores. *Am. Nat.* **153**, 492–508.
- PUTMAN, R. J. (1996): *Competition and resource partitioning in temperate ungulate assemblages*. London: Chapman and Hall.

- REYNOLDS, J. C.; AEBISCHER, N. J. (1991): Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Rev.* **21**, 97–122.
- SCHMIDT, R. H. (1986): Community-level effects of coyote population reduction. In: *Community Toxicity Testing*, ASTM STP 920. Ed. by J. CAIRNS, JR. Philadelphia: Am. Society for Testing and Materials. Pp. 49–65.
- SMITS, C. M. M.; SLOUGH, B. O.; YASUI, C. A. (1989): Summer food habits of sympatric arctic foxes, *Alopex lagopus*, and red foxes, *Vulpes vulpes*, in the northern Yukon Territory. *Can. Field-Nat.* **103**, 363–367.
- STRAND, O.; LANDA, A.; LINNELL, J. D. C.; SKOGLAND, T. (1998 b): Rødrevens fortrenning av fjellrev: interspesifikk konkurranse i naturlig fragmentert habitat. NINA temahefte **8**, 50–54.
- STRAND, O.; LINNELL, J. D. C.; KROGSTAD, S.; LANDA, A. (1998 a): Fjellrevens svar på endringer i smånager tetthet. NINA temahefte **8**, 61–64.
- TANNERFELDT, M.; ANGERBJÖRN, A. (1998): Fluctuating resources and the evolution of litter size in the arctic fox. *Oikos* **83**, 545–559.
- THEBERGE, J. B.; WEDELES, C. H. R. (1989): Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. *Can. J. Zool.* **67**, 1285–1290.

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